THE STRUCTURE OF THE WOOD IN THE PINEAE[1]

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(WITH PLATE V)

The Abietineae have been conveniently divided into the subfamilies Pineae and Abieteae.[2] The former are characterized by the presence of resin canals in the xylem, by their thinly integumented ovules, and by the non-deciduous character of the cone scales. The Abieteae differ in having resin canals absent from the woody tissues of the stem (except in the first annual ring of vigorous shoots of vigorous specimens of Abies), and by possessing usually a thick-coated ovule and deciduous cone scales. In both subfamilies resin canals may occur traumatically. These are easily differentiated from those normal to the stem by the fact that they occur in tangential rows of numerous canals, intercommunicating tangentially, and composed of generally heavily pitted epithelial cells. The Pineae comprise the genera Pinus, Picea, Larix, and Pseudotsuga. The Abieteae include Abies, Tsuga, Cedrus, and Pseudolarix. It will be the object of the present article to consider the structure of the woody cylinder in the former subfamily.

The four genera of the Pineae have been classified, by various authorities, according to the anatomical structure of the xylem as follows.

PINUS

The wood is characterized by the presence of numerous resin canals with thin-walled epithelium. This condition is constant except in the nut pines and foxtail pines of the southwestern United States, where thick-walled epithelial cells are interspersed among the usually thin-walled type. Further, Pinus is supposed to be characterized by the entire absence of wood-parenchyma, and according to GOTHAN of spiral thickenings of the tracheid walls of the secondary wood.[3]

[1] Contributions from the Phanerogamic Laboratories of Harvard University, No. 15.

[2] JEFFREY, The comparative anatomy and phylogeny of the Coniferales. Part 2. The Abietineae. Mem. Boston Soc. Nat. Hist. **6**:21. 1905.

[3] GOTHAN, Zur Anatomie lebender und fossiler Gymnospermen-Hölzer. Abhandl. König. Preuss. Geol. Landesanstalt. Neue Folge, Heft 44, p. 99. Berlin. 1905.

The pines are divided into the hard pines and the soft pines. The former are characterized by possessing dentate or reticulate tracheids of the rays, and by having no tangential pits developed in the tracheids at the end of the year's growth. The soft pines, on the contrary, are supposed to possess marginal and interspersed tracheids of the rays with unsculptured walls, and to have well-developed tangential pits in the tracheids formed at the end of the year's growth. The majority of the hard pines and soft pines can easily be separated from the remaining genera of the Pineae by the character of the pits in the lateral walls of the parenchymatous cells of the rays. These pits are very large and often polygonal, and quite distinct from the small round pits of Picea, Larix, and Pseudotsuga. However, in the nut and foxtail pines above referred to, and in certain of the hard pines, we find a diminution in the size of the pits, which approaches the condition in the Picea type.

PICEA

Picea has a wood with thick-walled epithelial cells in the resin canals and tangential pits in the summer tracheids. The pits in the lateral walls of the ray cells are small and round. The wood-parenchyma is entirely absent. Spiral thickenings of the tracheids are also absent, according to PENHALLOW.[4] However, GOTHAN (*op. cit.* 98) and other European authorities note their presence in the summer wood alone.

LARIX

The wood resembles Picea as regards the thick-walled character of the resin canals, the presence of tangential pits in the summer tracheids, and the small size of the lateral pits of the ray cells; but possesses well-developed wood-parenchyma upon the outer surface of the summer wood. Spiral thickenings of the tracheids are present only in the summer wood.

PSEUDOTSUGA

The wood resembles Picea and Larix as regards thick-walled epithelium, tangential pits of the summer tracheids, and form and size of the pits of the ray cells. It also resembles Larix in having parenchyma well developed upon the outer surface of the summer wood. The wood, however, is supposed to be quite distinct in having well-

4 PENHALLOW, North American Gymnosperms 195. Boston. 1907.

developed spiral thickenings in the spring as well as the summer tracheids. Further, according to MAYR,[5] spirals are also present in the ray tracheids of *Pseudotsuga macrocarpa* Mayr, but not in *P. Douglasii* Carr.

With this review of the generally accepted classification of the Pineae, let us turn to a careful consideration of the occurrence of each of the anatomical characters referred to above. In the first place as regards

WOOD-PARENCHYMA

As stated above, these cells are supposed to exist on the outer surface of the summer wood in Larix and Pseudotsuga, and to be entirely absent from Pinus and Picea. The presence of wood-parenchyma on the face of the summer wood in the xylem of a specimen of *Picea excelsa* Link in the Harvard Botanical Gardens led me to study this tree, believing that it was an unusual or freak specimen. The examination of sections from the root and stem showed the parenchyma well developed at the end of the year's growth (*figs. 1–3*), but in many cases the parenchymatous cells were rare or apparently absent from the stem. However, numerous sections cut from the same piece of wood always revealed one to several cells. It is difficult to see them in a transverse section, as they can be distinguished with certainty only when the simply pitted walls are visible. Obviously, to obtain this condition when the cells are rare is difficult. Likewise, in radial sections it is not easy to find them. If, however, tangential sections are cut in a slightly oblique manner, several layers of summer wood are visible in a single section. Many sections cut in series would then be more liable to reveal the presence of parenchymatous cells even when occurring infrequently. Cutting the sections in series avoids the possibility of confusing the parenchyma, for which I was searching, with that associated with resin canals or wound callus. However, the appearance of the latter as well as their location (not confined to the outer layer of the summer wood) is sufficient for their identification without these precautions.

I decided to use this method in the examination of other specimens of *Picea excelsa*, to see if wood-parenchyma were characteristic of the species. Upon examination it was found that the cells were present

[5] MAYR, Die Waldungen von Nordamerikas 424. *pl. 9*. München. 1890.

in *Picea excelsa* vars. *monstrosa*, *conica*, *elata*, *pendula*, and *pyramidalis*. Finding them characteristic of these varieties of the commonly planted *Picea excelsa*, it was decided to extend the studies to other species. Through the courtesy of Professor JACK, of the Arnold Arboretum, I was able to secure carefully identified green material of seventeen species of American, Asiatic, and European spruces. Thin serial sections of this material showed that the presence of wood-parenchyma upon the outer surface of the summer wood is a characteristic condition for Picea. Its occurrence, however, is extremely sporadic. In any given fragment of wood the cells may or may not appear, and while usually occurring very infrequently, may at any time appear in large numbers. These cells appeared more numerously in the European and Asiatic species, and in *Picea sitchensis* Carr. and *Picea Parryana* Sarg. of the American species. In the spruces from the northeastern United States they could be made out only with difficulty.

The extremely variable occurrence of wood-parenchyma is also characteristic of Larix and Pseudotsuga, for though usually occurring numerously upon the outer surface of the summer wood, in many specimens they may be very infrequent or nearly absent.

SEPTATE TRACHEIDS

In the three genera of the Pineae just mentioned septate tracheids occur with the parenchyma upon the outer surface of the year's growth. In Picea they are usually more numerous than the wood-parenchyma and occur where wood-parenchyma is not developed. In Larix and Pseudotsuga the parenchyma usually predominates. There is a clear gradation shown from tracheid to parenchyma in these genera. Frequently one may observe in the same section a septate tracheid, a tracheid partly septate and partly parenchymatous (*fig. 4*), and a series of resin cells, together having the form of a tracheid. In other words, the various steps by which tracheids have been modified to form parenchyma are clearly shown. In support of these statements it may be well to add that primitive woods were composed entirely of tracheids and medullary parenchyma, and that only in the higher gymnosperms do we see the development of wood-parenchyma, first upon the outer surface of the summer wood, and later throughout

the year's growth in plants which have lost, or are in the process of losing, their resin canals. In the Pineae, in which resin canals occur normally, the parenchyma is confined to the end of the year's growth, and less well developed in the older genera, which have more numerously developed resin canals. Thus Pinus, with its large supply of resin canals, shows only the first steps in the development of wood-parenchyma. Septate tracheids occur infrequently upon the outer surface of the summer wood, and only in one instance have I been able to observe what appeared to be parenchyma in the same location. In Picea, with less well-developed resin ducts, the wood-parenchyma becomes constant, while in Larix and Pseudotsuga it is usually strongly developed. In the Taxodineae and Cupressineae, with the nearly complete disappearance of resin canals, the wood-parenchyma is well developed throughout the year's growth, as well as at the end of the summer wood. The Abieteae are transitional between the two groups. It seems probable, as JEFFREY has suggested in his paper on the Abietineae (*op. cit.* 26), that with the reduction of foliage in the Abietineae and Cupressineae, the freely anastomosing system of canals, with its large supply of resinous secretions for sterilizing wounds, became too great a burden, and that the system of resin cells was gradually developed to take its place. It is not my object to enter here into all the various phases of the controversy as to the age of the Abietineae, but recent paleontological evidence proves the great geological age of Pinus. Further, Prepinus is a primitive abietineous type with centripetal wood, resembling certain of the Cordaites, and at the same time closely allied to the true pines of the middle Cretaceous.[6] A survey of all the paleontological evidence, as well as a study of the anatomy and morphology of the modern Coniferales, seems to show conclusively the greater age of the Abietineae.

SPIRAL THICKENINGS

Let us now turn to a consideration of the occurrence and distribution of tertiary thickenings of the tracheid walls in the Pineae.[7] As stated above, PENHALLOW considers spiral thickenings absent from

[6] JEFFREY, Structure of the leaf in Cretaceous pines. Annals of Botany 21:207–220. *pls. 13, 14.* 1908.

[7] It should be kept clearly in mind that these spirals are tertiary thickenings, and are entirely distinct from the so-called "spiral striations" of the secondary walls of the tracheids.

Picea, while European authorities note their presence only in the summer wood. In the seventeen species of Picea which I examined, I found spirals well developed in the summer wood of the first few years' growth, usually from the first or second to the tenth year. In older woods they are very sporadic in their development, in certain regions appearing well developed, but usually showing at best only feebly. In wounded areas they showed a tendency to be strongly developed. In two species, *Picea sitchensis* Carr. and *Picea Maximowiczii* Regel, the spirals were very strongly developed in the spring as well as the summer wood (*fig. 6*). Furthermore, in both of these species, spiral thickenings were well developed in the marginal and interspersed tracheids of the rays (*fig. 5*). They occurred in the ray tracheids in both the summer and spring wood. In other species of Picea this condition could be made out in the tracheids of the rays of the summer wood. In other words, the ray tracheids appear to follow closely the wood tracheids. Where spirals are strongly developed in the latter elements, they will appear usually in the former.

In Larix the spirals were observed occurring in the first few years' growth, but not so well developed as in Picea. In the mature wood and in the ray tracheids, the spirals are likewise sporadic in their appearance, and may or may not be noticeably developed. Only four species were examined, *Larix americana* Michx., *L. europaea* DC., *L. occidentalis* Nutt., *L. dahurica* Turcz., and in none of these were spirals present in the spring wood; yet from the similarity to Picea and Pseudotsuga I should consider it extremely likely that they would be found, if a large amount of material were examined.

In Pseudotsuga spirals occur in both the summer and spring tracheids, yet they also are sporadic in their development, in certain specimens appearing well marked throughout, or in others nearly absent. MAYR notes the presence of spiral thickenings in the marginal tracheids of *Pseudotsuga macrocarpa* Mayr, but states (*loc. cit.*) that they are absent in *P. Douglasii* Carr. Sections from specimens of the Douglas fir from various sources show the spirals well developed in the marginal tracheids of certain specimens and less well developed in others.

In Pinus, as has been noted, GOTHAN asserts the absence of spirals, yet PENHALLOW (*op. cit.* 41) has described them as occurring in

Pinus taeda Linn., and I have myself observed them in *Pinus attenuata* Lemm. and several other species. Furthermore, spiral thickenings occur in the ray tracheids of *Pinus Balfouriana* A. Murr.; they are strongly developed in certain specimens and only feebly in others. *Pinus strobiformis* Engelm. and other pines from the southwestern United States show traces of their occurrence.

From the development of the spirals of the tracheids in the first year's growth and in areas of injury, it would appear that the spirals were an early development, yet the fact that they are not always present in the first and second annual rings, and are absent from the axis of the cone, would seem to show that the character cannot be primitive. It certainly would not be safe to assume that the presence of these spirals is an indication of close relationship with the Taxaceae, for spiral thickenings of the vessels in the dicotyledons are found in such widely separated families as the Betulaceae and Tiliaceae.

INSTABILITY OF DIAGNOSTIC CHARACTERS

From the preceding remarks on the development of wood-parenchyma and spiral thickenings, and the sporadic and uncertain character of their appearance, one realizes the difficulty in finding any definite basis upon which to separate Picea, Larix, and Pseudotsuga. As has been shown, one can no longer depend upon the presence or absence of wood-parenchyma and spirals to acomplish this end.

Let us now turn to consider the stability of the other elements of the wood. The size, form, and location of the resin canals vary so greatly in material from different sources that no rule can be formulated to cover every case. It is true that Picea approaches nearer to the condition found in the nut and foxtail pines than the other genera. Thus certain spruces have considerable thin-walled epithelium and tyloses, yet thin-walled epithelium occurs in Larix and Pseudotsuga. Further, the same variability is characteristic of the pitting of the rays and tracheids, and of the weight and color of the wood. We are thus forced to the conclusion that in order to distinguish the woods of Picea, Larix, and Pseudotsuga, a careful study must be made of all the anatomical and gross characters, and comparisons made with type sections. In other words, one must apply here the same methods in differentiating genera which one usually uses in distinguishing species.

As an illustration of the difficulty in distinguishing these woods let us consider a fossil from California recently described by GOTHAN.[8] He identifies the specimen as follows. The fact that the resin canals are typically non-pine-like, with thick-walled epithelium, shuts out Pinoxylon. The presence of wood-parenchyma and spirals in the spring wood shows its relation to Pseudotsuga. *Pseudotsuga macrocarpa* has ray tracheids with spirals, and in *P. Douglasii* they are absent. Thus the fossil, which he calls *Piceoxylon Pseudotsugae*, as it has no spirals in the ray tracheids, must be closely allied to the Douglas fir, if not a fossil specimen of it.

In the first place, as we have seen, *Pseudotsuga Douglasii* possesses spiral thickenings in the ray tracheids. This, according to the author's own line of reasoning, would exclude *P. Douglasii*. Further, let us consider the statements in regard to the presence of wood-parenchyma and spiral thickenings in the spring wood. As has been shown above, both these conditions occur in *Picea sitchensis*, a spruce from the Pacific coast. Can we be sure whether this fossil is more closely allied to Pseudotsuga, Picea, or even Larix? As an added reason for regarding the fossil allied to Pseudotsuga, the author states that the horizontal resin canals in the fusiform rays occur in an unsymmetrical manner. This same condition may be frequently observed in both Picea and Larix. One comes to the conclusion that the identification of woods and fossils of Picea, Larix, and Pseudotsuga is an extremely difficult undertaking.

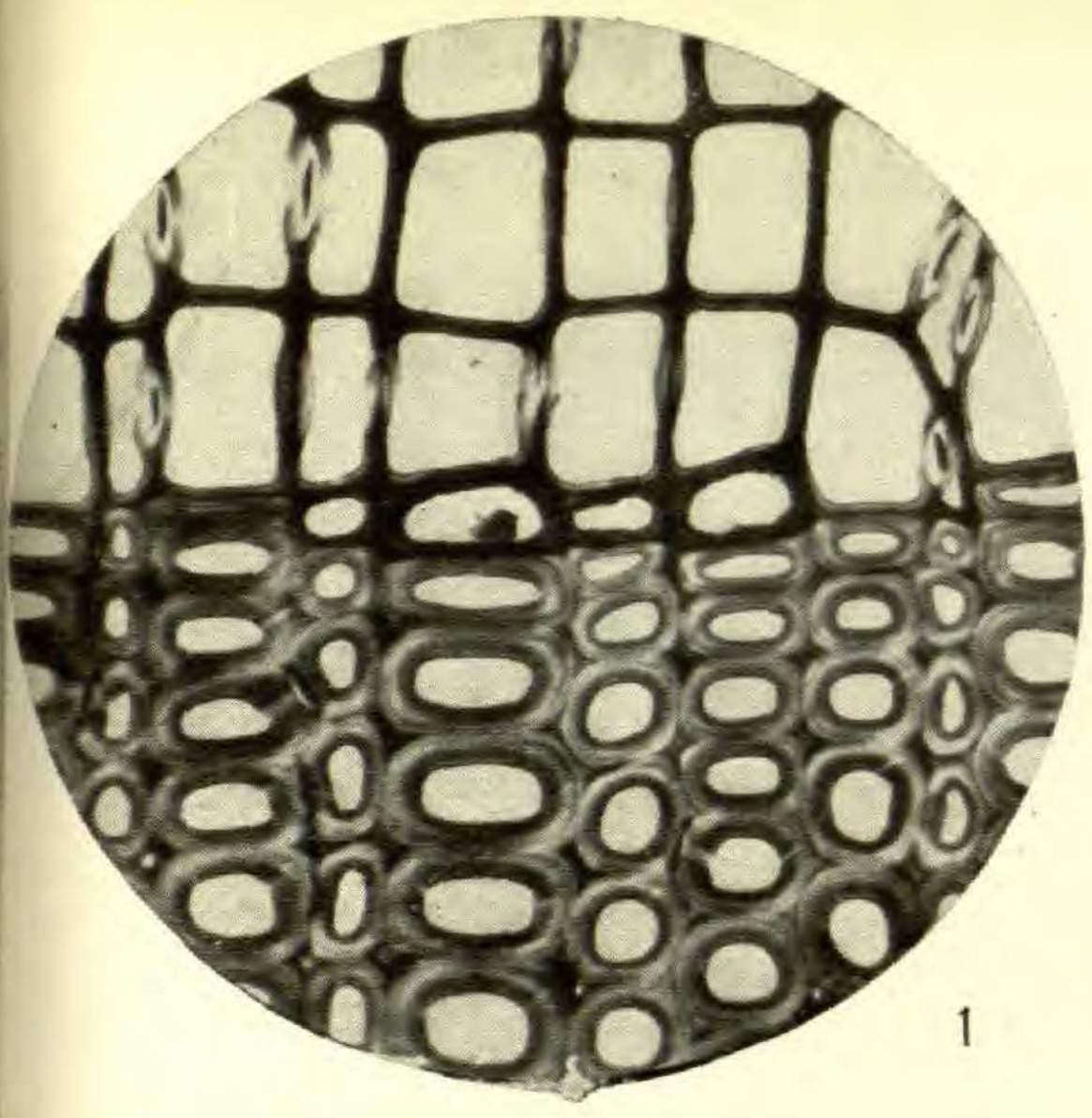
SUMMARY

1. Wood-parenchyma occurs on the outer surface of the summer wood of Picea. It is sporadic in its occurrence, and while usually appearing infrequently, may be strongly developed.

2. Wood-parenchyma may be very sparsely developed in Larix and Pseudotsuga.

3. Septate tracheids occur associated with the wood-parenchyma in these three genera, and show clearly the steps by which wood-parenchyma has been developed from tracheids.

[8] GOTHAN, *Piceoxylon Pseudotsugae* als fossiler Holz, *Pseudotsuga* sp. (aff. *Douglasii*) als rezenter Baum; in H. POTONIE, Abbildungen u. Beschreibungen Foss. Pflanzen, Lief 4. 1906.



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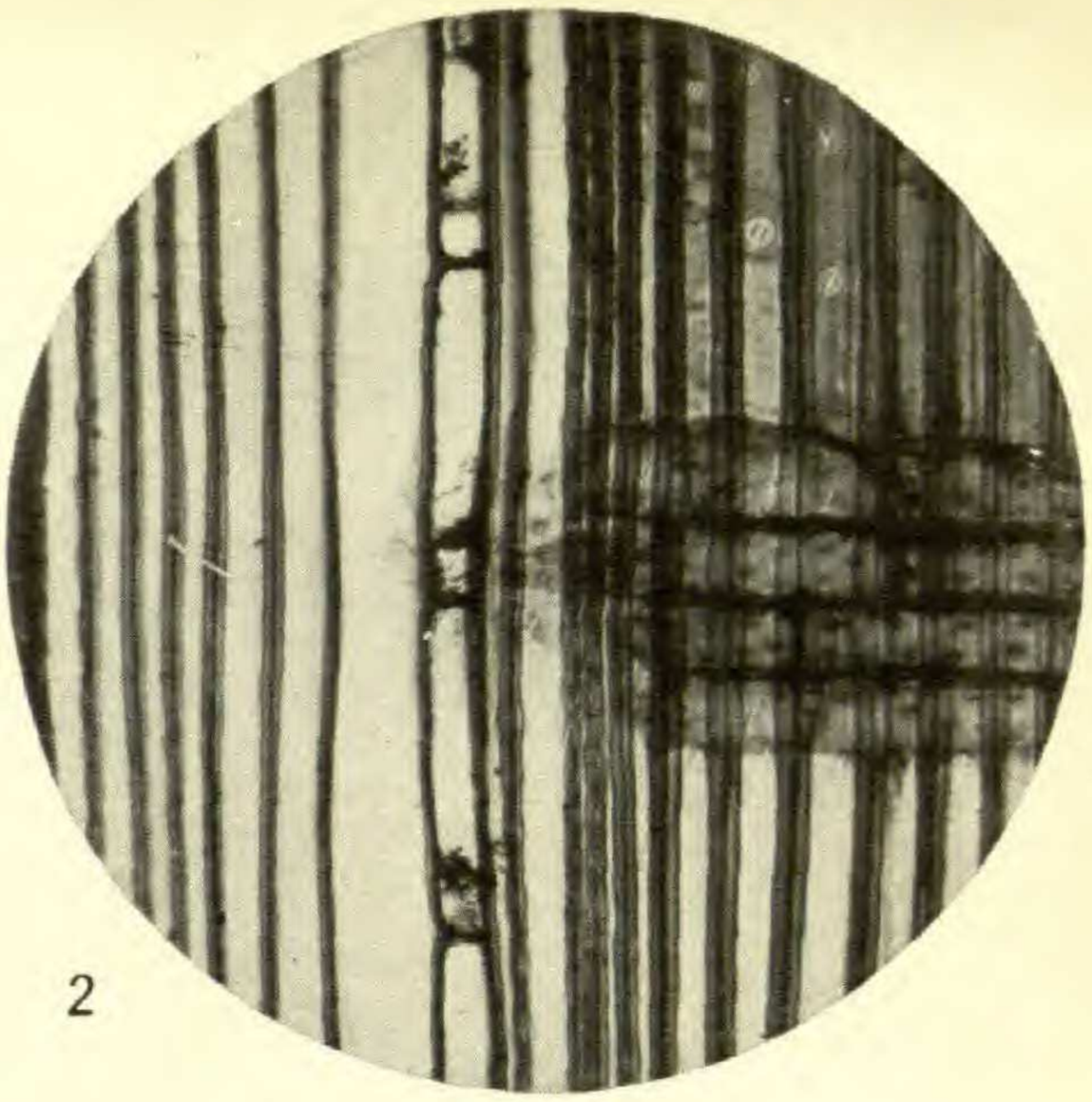

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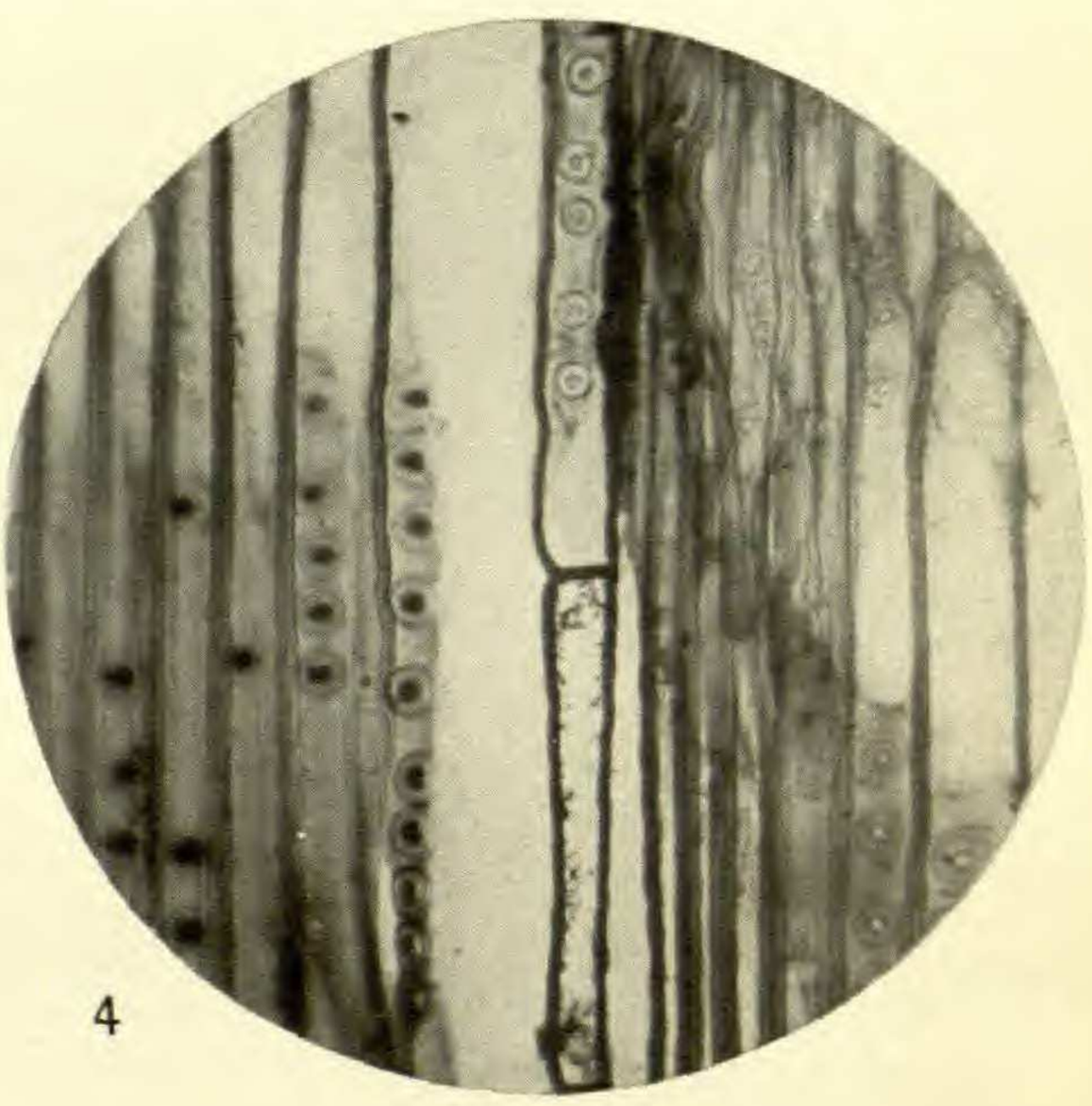

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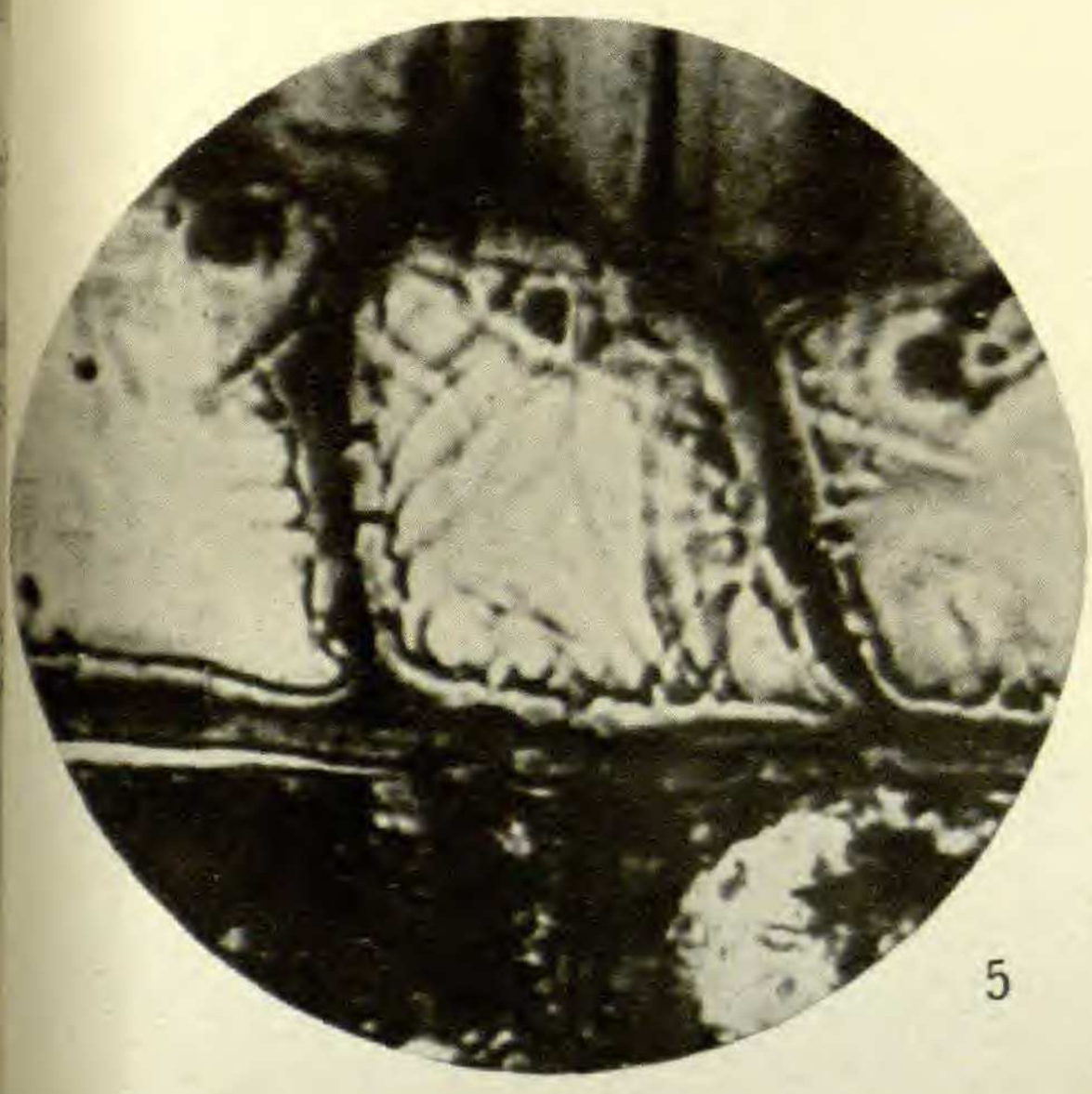

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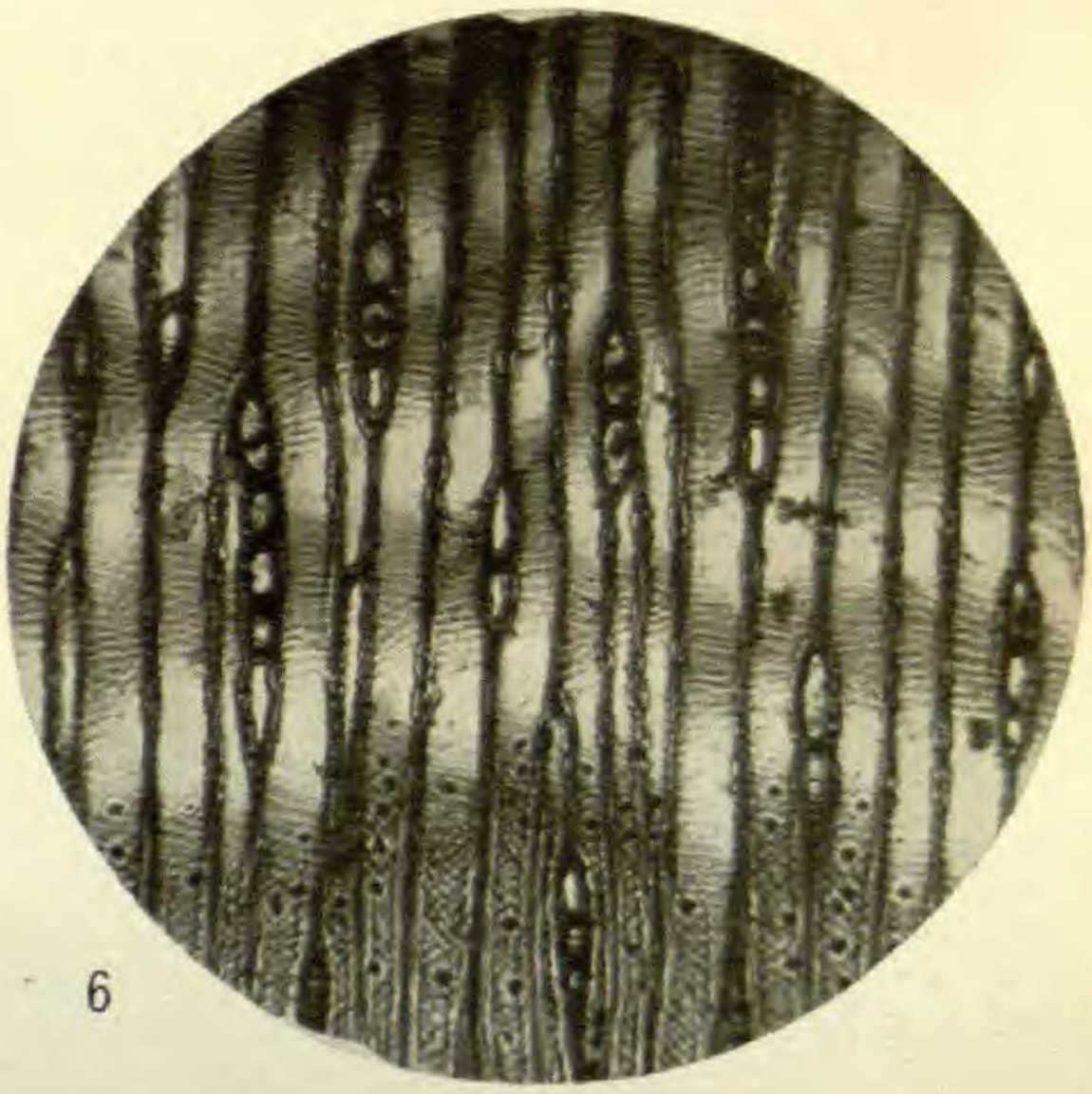

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BAILEY on WOOD OF PINEAE